

# Phase transition and selection in a four-species cyclic Lotka-Volterra model

György Szabó

Research Institute for Technical Physics and Materials Science P.O. Box 49, H-1525 Budapest, Hungary

Gustavo Ariel Sznaider

Centro de Servicios Informáticos and IFEVA, Faculty of Agronomy,  
University of Buenos Aires, Av. San Martín 4453, Buenos Aires (1417), Argentina

(Dated: February 9, 2008)

We study a four species ecological system with cyclic dominance whose individuals are distributed on a square lattice. Randomly chosen individuals migrate to one of the neighboring sites if it is empty or invade this site if occupied by their prey. The cyclic dominance maintains the coexistence of all the four species if the concentration of vacant sites is lower than a threshold value. Above the threshold, a symmetry breaking ordering occurs via growing domains containing only two neutral species inside. These two neutral species can protect each other from the external invaders (predators) and extend their common territory. According to our Monte Carlo simulations the observed phase transition is equivalent to those found in spreading models with two equivalent absorbing states although the present model has continuous sets of absorbing states with different portions of the two neutral species. The selection mechanism yielding symmetric phases is related to the domain growth process with wide boundaries where the four species coexist.

PACS numbers: 05.50.+q, 87.23.Cc

Multispecies ecological models with spatial extension exhibit a large variety of possible stationary states as well as phase transitions when tuning the model parameters. In the original Lotka-Volterra models [1, 2] as well as in the generalized versions the spatial distribution of species is neglected (see [3, 4] for reviews). Now we report a phenomenon underlying the role of spatial effects in the biological evolution.

In the simplest spatial Lotka-Volterra models the individuals of competitive species are residing on the sites of a lattice and the system evolution is governed by invasions along the nearest neighbor links. In many cases the species form domains with growing sizes and sooner or later only one species will survive. Significantly different behavior is found if the species dominate cyclically each other, i.e., the corresponding food web is characterized by a directed ring graph [5, 6, 7]. Frachebourg and Krapivsky [6] have shown that fixation occurs if the number of species  $N_s$  exceeds a threshold value  $N_f(d)$  depending on the spatial dimension  $d$ . In this case the species form a frozen domain structure [6]. Conversely [ $N_s \leq N_f(d)$ ], the moving invasion fronts maintain a self-organizing polydomain structure. These patterns are widely studied for  $N_s = 3$  [5, 8, 9] because it can provide a stability against some external invaders for the spatial models [10, 11, 12]. Sato *et al.* [13] have shown that, if only one of the invasion rates differs from unity for even  $N_s$ , then only the species with odd (even) labels survive. Very recently, the species biodiversity were studied by similar models in bacterial [14], phytoplankton [15] systems.

In the above lattice models each site is occupied by an individual of the competitive species. Now we will consider a diluted version of these models for  $N_s = 4$ . Namely, the sites may be empty and the individuals are allowed to jump to these empty sites. These elementary events can result in the formation of “defensive alliances” consisting of two neutral species. These two-species mixed states can preserve their territory from the external invaders belonging to the remaining

two species. Thus, beside the above mentioned four-species state, this model has two sets of “defensive alliances” whose confrontations will determine the final stationary state. When increasing the concentration of vacant sites this system undergoes a phase transition from the symmetric four-species state to one of the symmetric defensive alliances. This transition will be interpreted by considering the average displacement (and velocity) of boundary separating two competitive domains.

In the present model the site  $i$  of a square lattice can be empty ( $s_i = 0$ ) or single occupied by one of the four species (i.e.,  $s_i = 1, 2, 3$ , and 4) dominating cyclically each other (1 beats 2 beats 3 beats 4 beats 1). The time evolution is controlled by subsequent jumps or invasions at randomly chosen nearest neighbor sites  $i$  and  $j$ . The individual will jump to the empty site, i.e., the value of  $s_i$  and  $s_j$  are exchanged ( $s_i \leftrightarrow s_j$ ) if  $s_i = 0$  and  $s_j > 0$  or  $s_i > 0$  and  $s_j = 0$ . Invasion occurs if predator and prey meet. For example, both the (1,2) and (2,1) pairs transform into (1,1) [the further elementary invasions are given by cyclic permutation of the species labels]. Nothing happens if  $s_i = s_j$  as well as for neutral pairs, i.e., the pairs (1,3), (3,1), (2,4), and (4,2) remain unchanged. The system is started from a random initial state. After some transient time the system reaches a stationary state we study.

Notice that the above elementary rules leave the number of vacant sites unchanged and their distribution becomes uncorrelated after a suitable relaxation time. The states containing only one species are considered as absorbing states because the above rule does not create new species. Besides this, the mixed states containing only two neutral species (1+3 or 2+4) are also absorbing states and will be denoted as  $D_{13}$  and  $D_{24}$ . In these stationary states the ratio of the two species remains constant. In the presence of vacant sites the migration eliminates the spatial correlations. For small sizes this system can easily reach one of these absorbing states and afterwards it stays there forever.

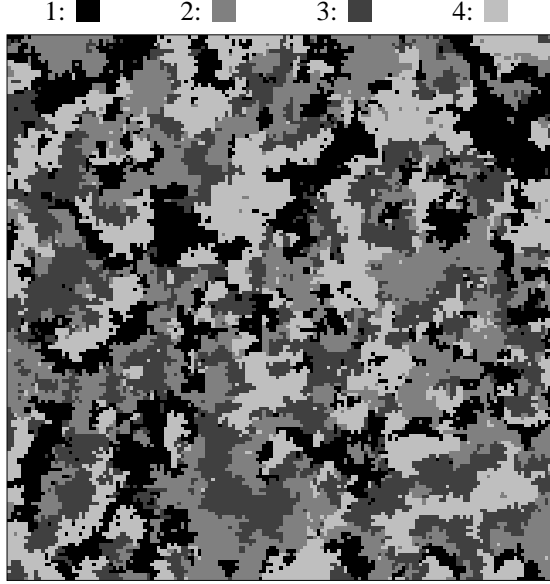


FIG. 1: Spatial distribution of the four species on the square lattice if  $\rho_0 = 0$ . The grayscale of the four species are indicated above the snapshot.

Our Monte Carlo (MC) simulations are performed on a square box with periodic boundary conditions. In order to avoid the above mentioned small size effect the linear size is varied from  $L = 400$  to  $2000$ . The systematic simulations are started from a random initial state for different concentration of vacant sites ( $\rho_0$ ). Within a time unit (MCS) each pair has a chance once on the average to modify the state at one of the corresponding sites. During the simulations we have recorded the concentration of species and the pair configuration probabilities on the nearest neighbor sites. Averaging over a suitable sampling time interval we have determined the average species concentrations ( $\rho_\alpha$ ,  $\alpha = 1, 2, 3$ , and  $4$ ). Furthermore, we have deduced two quantities  $P_{pp}$  and  $P_n$  describing the probability of finding predator-prey and neutral pairs on two nearest neighbor sites. Evidently,  $P_{pp}$  measures the invasion activity that vanishes in the absorbing states.

The visualization of species distribution shows a self-organizing polydomain structure in the absence of vacant sites (for a typical snapshot see Fig. 1). The species occur cyclically at each sites, however, the short range interaction can not synchronize these accidental events. In the pattern evolution one can easily recognize the traveling invasion fronts that play crucial role in the maintenance of this polydomain structure [5, 9]. Similar spatiotemporal patterns can be observed for low concentration of vacant sites. Henceforth this spatiotemporal pattern is called  $C$  state.

In the stationary  $C$  state  $\rho_1 = \rho_2 = \rho_3 = \rho_4 = (1 - \rho_0)/4$  due to the cyclic symmetry. Strikingly different behavior occurs if  $\rho_0 > \rho_{cr} = 0.0623(1)$ . When using lighter (darker) grayscales for the species 1 and 3 (2 and 4) two types of growing domains (namely  $D_{13}$  and  $D_{24}$ ) can be distinguished as shown in Fig. 2. These growing domains are separated by wide regions of  $C$  states. The growth process is similar

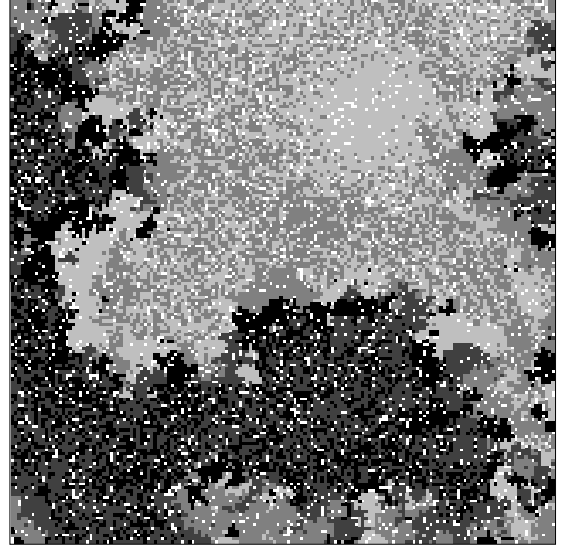


FIG. 2: Typical domain structure at time  $t = 3000$  MCS (Monte Carlo steps per sites) if initially ( $t = 0$ ) the spatial distribution was random for  $\rho_0 = 0.1$ . The white boxes refer to empty sites while the grayscale of species as in Fig. 1.

to those observed in systems with two equivalent absorbing states [16, 17, 18, 19]. Finally the present system develops into one of the symmetric two-species absorbing states  $D_{13}$  or  $D_{24}$  where  $\rho_1 = \rho_3 = (1 - \rho_0)/2$  and  $\rho_2 = \rho_4 = 0$ , or  $\rho_2 = \rho_4 = (1 - \rho_0)/2$  and  $\rho_1 = \rho_3 = 0$ . The time of transition toward one of these states depends on  $\rho_0$  and  $L$ . Both the species 1 and 3 benefit their spatially mixed coexistence because they protect each other from the external invasions. For example, the species 2 can invade the sites occupied originally by species 3, however, the neighboring species 1 strikes back and eliminates the invaders 2. At the same time, species 3 protects 1 against 4. This is the reason why this association is called defensive alliance. Due to the cyclic symmetry species 2 and 4 can form a similar defensive alliance.

The formation of defensive alliances was already observed in some other multispecies Lotka-Volterra model where the cyclic invasion itself has provided the protection mechanism [11, 12]. In the present model, however, the protection is due to the mixing of neutral species via the jumps to empty sites.

Figure 3 demonstrates that the probability of neutral pairs ( $P_n$ ) increases with the concentration of vacant sites in the stationary states. Above the mentioned threshold value ( $\rho_0 > \rho_{cr}$ ) this quantity tends to the uncorrelated value,  $P_n = (1 - \rho_0)^2/2$ , characteristic to the symmetric defensive alliance state. Simultaneously, the invasion activity (or  $P_{pp}$ ) decreases and drops suddenly to zero at  $\rho_0 = \rho_{cr}$ . The discontinuous transition is accompanied with enhanced fluctuations (in all the quantities we studied) and a critical slowing down. To avoid the undesired effects of fluctuation enhancements, the above MC data have been obtained on large system ( $L = 2000$ ) with long relaxation and sampling times ( $t_r > 10^4$  MCS and  $t_s > 10^5$  MCS) in the close vicinity of the transition point.

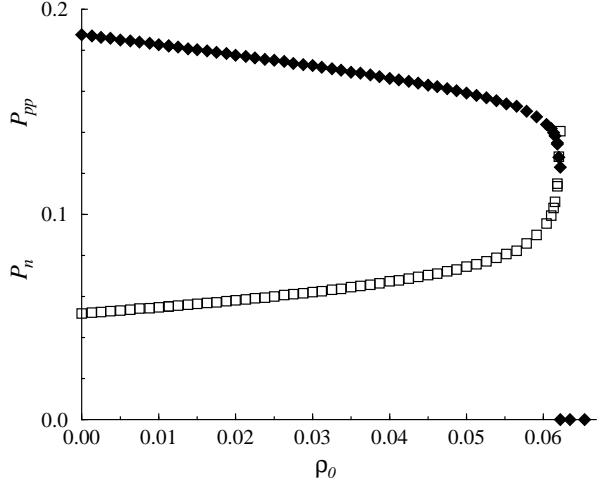


FIG. 3: Monte Carlo results for the probability of finding predator-prey (closed diamonds) and neutral pairs (open squares) on two nearest neighbor sites in the stationary states.

The universal behavior of the nonequilibrium transitions into absorbing states have extensively been studied for several decades (for a review see the Refs. [20, 21]). The dynamical systems with two equivalent absorbing states represent a curious universality class (named after the voter model) [16, 17, 18, 22, 23] whose general features are consistent to those described above.

To have a deeper insight into the dynamics of the present model we now will study the displacement of interfaces separating the  $C$  state and one of the stationary defensive alliances ( $D_{13}$  or  $D_{24}$ ). For the preparation of such an artificial domain structure the whole area (torus) is divided into parallel strips with width of 500 lattice units. The MC simulation is started from a random initial state (as above) for  $L = 4000$  and after a suitable relaxation time  $t_r$  uncorrelated  $D_{13}$  state is created in every second strip. More precisely, species 1 and 3 are substituted randomly for the occupied sites located inside the corresponding strips. First we consider the results obtained for symmetric distribution, i.e., when inside the defensive alliances ( $D_{13}$ )  $\rho_1 = \rho_3 = (1 - \rho_0)/2$ . The expansion (or shrinking) of the  $C$  domains can be monitored by evaluating the quantity  $\Phi(t) = \rho_1(t) - \rho_2(t) + \rho_3(t) - \rho_4(t)$ . Notice that  $\Phi$  vanishes ( $\langle \Phi \rangle = 0$ ) for the state  $C$  whereas  $\Phi(t) = \pm(1 - \rho_0)$  in the absorbing states. The average displacement (measured in lattice unit) of the parallel interfaces are derived straightforwardly from the variation of  $\Phi(t)$ .

Figure 4 displays the typical time dependences of the average displacement  $d(t)$  of the boundaries separating the  $C$  and  $D_{13}$  states. The increase of  $d(t)$  corresponds to the expansion of  $C$  domains. The MC data are obtained by averaging over 20 runs performed for  $L = 4000$  and  $t_r = 3000$  MCS if  $\rho_0 < \rho_{cr}$ . Above the critical point ( $\rho_0 > \rho_{cr}$ ) we have to use significantly shorter relaxation times ( $t_r = 200$  MCS) to avoid the difficulties caused by the appearance of the  $D_{13}$  and  $D_{24}$  nucleons. It is remarkable that at the beginning  $d(t)$  decreases suddenly. After a suitable transient time, however,

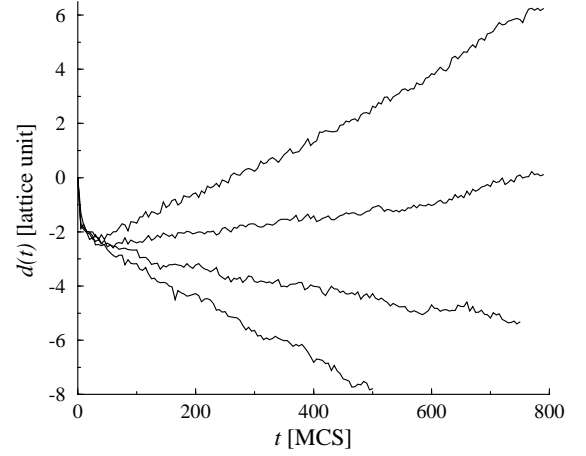


FIG. 4: Average displacement of boundaries between the states  $C$  and  $D_{13}$  as a function of time for  $\rho_0 = 0.056, 0.060, 0.064$ , and  $0.070$  (from top to bottom).

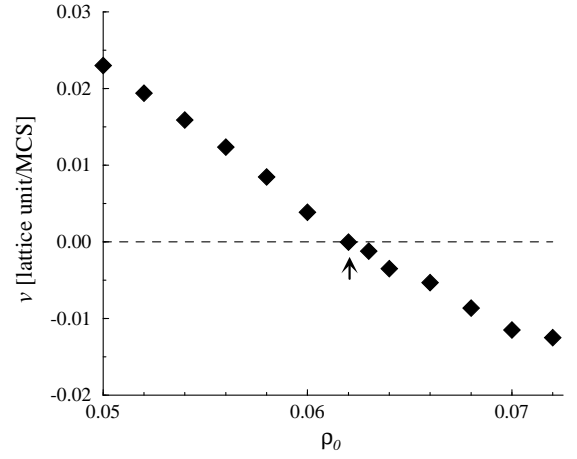


FIG. 5: Average velocity of invasion front between the states  $C$  and  $D_{13}$  as a function of the concentration of vacant sites. The arrow indicates the critical point derived from the investigation of the stationary states. The statistical error is comparable to the symbol size.

the variation of  $d(t)$  becomes linear and the fitted slope can be interpreted as the average velocity  $v$  of the invasion front.

Figure 5 clarifies that the  $C$  state invades the territories of defensive alliances for low concentration of vacant sites. The average invasion velocity decreases monotonously with  $\rho_0$  and becomes zero at  $\rho_0 = \rho_{cr}$ . In agreement with the expectation, the area of the  $C$  domains shrinks for  $\rho_0 > \rho_{cr}$ .

The above simulations were repeated by choosing asymmetric compositions (e.g.,  $\rho_1 > \rho_3$ ) within the  $D_{13}$  state. It is found, that the asymmetry has influenced only the short time behavior. For example, if  $\rho_1 \gg \rho_3$  then the  $C$  state can invade fast ( $v \sim 1$ ) those neighboring patches occupied by only the species 1 in the  $D_{13}$  domains. Consequently, in this case one can observe a sudden increase (instead of decrease as plotted in Fig. 4) in  $d(t)$ . In the subsequent linear region, however the average velocity  $v$  becomes independent of  $(\rho_1 - \rho_3)$  within

the statistical error. The visualization of the species distribution has indicated that the boundary between the  $C$  and  $D_{13}$  domains fluctuates very intensively. In fact, it is not a well defined boundary because the sites occupied by species 1 and 3 can belong to both phases within a boundary layer. Within this boundary layer the cyclic invasions sustain the equivalence between  $\rho_1$  and  $\rho_3$  on average for long times. This boundary layer can be considered as a symmetric species reservoir that drives an equalization between the different species concentration in the asymmetric  $D_{13}$  phase via diffusion.

This scenario is checked by considering the evolution from such an initial state where the parallel strips (created as above) are filled alternately by the symmetric  $D_{24}$  and asymmetric  $D_{13}$  states. The simulations (for  $\rho_0 > \rho_{cr}$ ) have confirmed that the variation of  $d(t)$  is similar to a random walk meantime the difference  $\rho_1 - \rho_3$  tends to zero for long times. This is the reason why we have always found symmetric  $D_{13}$  or  $D_{24}$  states after the domain coarsening process for sufficiently large system sizes. At the same time this phenomenon can be interpreted as a selection mechanism favorizing the symmetric defensive alliances.

Here it is worth mentioning that the traditional mean-field and pair approximations (for details see [20, 24]) are capable to reproduce the existence of the above mentioned absorbing states. However, these techniques are not capable to describe the observed phase transition. We think that this failure is due to the very complex mechanisms consisting of many elementary steps within a local cycle.

In summary, our work shows that a slight migration in the lattice Lotka-Volterra models may significantly affect the species biodiversity. Dilution and migration are attributes usually found in ecosystems whose description should include these features. The present model exemplifies that the migration of species supports the formation defensive alliances

in the multispecies ecological systems. Furthermore, the confrontation between the different associations of species plays crucial role in the selection of the survival population structure. In this case a phase transition occurs when the rate of migration is increased by allowing more and more vacant sites (and jumps) on the lattice.

The above described features are observed for many other systems. Preliminary results indicate clearly that similar behavior occurs if the mixing is provided by the site exchange for neutral pairs without introducing vacant sites. Furthermore, quantitatively similar behavior is found for the continuous version of the present model, i.e., when the individuals move freely on a planar surface and they create an offspring if they eat a prey caught within a short distance. In fact, this former finding inspired us to introduce a simpler model for the more rigorous analysis.

We think that the mixing of neutral species can results in other defensive alliances in multispecies systems. For example, two equivalent alliances are expected to emerge in the  $N_s$ -species model with a circular food web for even  $N_s$ . Evidently, such alliances can occur for more complicated food webs when the species have several preys and predators [11, 12]. In these situations the competition between the possible (defensive) alliances will affect the evolution of the ecological system including the food web itself [25, 26].

### Acknowledgments

Thanks to Diego Gomez Deck with whom one of us developed the earlier continuous version of the model. This work was supported by the Hungarian National Research Fund under Grant No. T-33098.

- 
- [1] V. Volterra, *Lecon sur la Theorie Mathematique de la Lutte pour la Vie* (Gouthier-Villars, Paris, 1931).
  - [2] A. J. Lotka, Proc. Natl. Acad. Sci. USA **6**, 410 (1920).
  - [3] J. Hofbauer and K. Sigmund, *Evolutionary Games and Population Dynamics* (Cambridge University Press, Cambridge, 1998).
  - [4] B. Drossel, Adv. Phys. **50**, 209 (2001).
  - [5] K. Tainaka, Phys. Rev. E **50**, 3401 (1994).
  - [6] L. Frachebourg and P. L. Krapivsky, J. Phys. A: Math. Gen. **31**, L287 (1998).
  - [7] K. Tainaka, Phys. Rev. Lett. **63**, 2688 (1989).
  - [8] G. Szabó, M. A. Santos, and J. F. F. Mendes, Phys. Rev. E **62**, 1095 (1999).
  - [9] G. Szabó and A. Szolnoki, Phys. Rev. E **65**, 036115 (2002).
  - [10] M. C. Boerlijst and P. Hogeweg, Physica D **48**, 17 (1991).
  - [11] G. Szabó and T. Czárán, Phys. Rev. E **63**, 061904 (2001).
  - [12] G. Szabó and T. Czárán, Phys. Rev. E **64**, 042902 (2001).
  - [13] K. Sato, N. Yoshida, and N. Konno, Appl. Math. Comp. **126**, 255 (2002).
  - [14] B. Kerr, M. A. Riley, M. W. Feldman, and B. J. M. Bohannan, Nature **418**, 171 (2002).
  - [15] J. Huisman and F. J. Weissing, Ecology **82**, 2682 (2001).
  - [16] R. Dickman and A. Y. Tretyakov, Phys. Rev. E **52**, 3218 (1995).
  - [17] H. Hinrichsen, Phys. Rev. E **55**, 219 (1997).
  - [18] I. Dornic, H. Chaté, J. Chave, and H. Hinrichsen, Phys. Rev. Lett. **87**, 045701 (2001).
  - [19] A. Mehta and J. M. Luck, Phys. Rev. E **60**, 5218 (1999).
  - [20] J. Marro and R. Dickman, *Nonequilibrium Phase Transitions in Lattice Models* (Cambridge University Press, Cambridge, 1999).
  - [21] H. Hinrichsen, Adv. Phys. **49**, 815 (2000).
  - [22] J. F. F. Mendes, R. Dickman, M. Henkel, and M. C. Marques, J. Phys. A: Math. Gen. **27**, 3019 (1994).
  - [23] M. A. Muñoz, G. Grinstein, and Y. Tu, Phys. Rev. E **56**, 5101 (1997).
  - [24] J. E. Satulovsky and T. Tomé, Phys. Rev. E **49**, 5073 (1994).
  - [25] R. D. Holt, Ecol. Res. **17**, 261 (2002).
  - [26] D. Chowdhury and D. Stauffer, cond-mat/0305322.